A NEW SPECIES OF STEM-GROUP CHORDATE FROM THE UPPER ORDOVICIAN OF NORTHERN IRELAND

by A. P. CRIPPS

ABSTRACT. A new scotiaecystid, *Scotiaecystis collapsa* sp. nov. is described from the Killey Bridge Beds, lower Cautleyan Stage, Ashgill Series, near Pomeroy, Co. Tyrone, Northern Ireland. It is most closely related to *S. curvata* Bather. The interrelations of cornutes are studied through a cladistic analysis using PAUP (Phylogenetic Analysis Using Parsimony) involving twenty-one species and thirty-nine characters. Three equally parsimonious trees are obtained and their information content summarized in the form of a consensus tree. By the addition of the mitrates (primitive crown-group chordates) this consensus tree is resolved. As in previous studies, the genus *Cothurnocystis* forms an uncharacterizable group with some species more crownward than others. The genus *Thoralicystis* is also paraphyletic. The Scotiaecystidae are an extinct monophyletic group more crownward than *C. elizae* Bather and less crownward than the Phyllocystidae, *Amygdalotheca*, and *Reticulocarpos*. The scotiaecystids exhibit a departure from a primitively deposit-feeding mode of life towards suspension feeding. The hind tail of *S. collapsa* is unusual for it is not truncated at the end as is often the case in other cornutes and is flexible in both the horizontal and vertical planes. The family Phyllocystidae is redefined to contain *Phyllocystis* and *Chauvelicystis*, and the family Cothurnocystidae redefined to include only *Cothurnocystis elizae* Bather, *C. courtessolei* Ubaghs, and *C. primaeva* Thoral.

THE aims of this paper are to describe a new species of stem-group chordate belonging to the plesion (family) Scotiaecystidae (Caster and Ubaghs, in Ubaghs 1967) and to provide a cladistic analysis of the cornutes. The cornutes and mitrates are controversial. More precisely, two groups are currently proposed as the living models for these fossil forms: the phylum Echinodermata (Ubaghs 1967; Philip 1979) and the phylum Chordata (Jefferies 1967). Whilst Ubaghs and Philip agree that cornutes and mitrates are echinoderms, their interpretations of the structure believed here to be the tail differ. Philip believed this organ to be a crinoid-type stem and called it a stele (although he accepted its locomotory function), but Ubaghs argued that it was an aulacophore or feeding arm. The interpretation of Jefferies, that these organisms were chordates, is adopted here. The detailed arguments for this view are found in Jefferies (1986).

PHYLOGENETIC METHODOLOGY AND CLASSIFICATION

The stem-group concept of Hennig (1965, 1969, 1981) is used here in order to place fossils in relation to extant groups when reconstructing phylogeny. Except for the case of a genuine polytomy, every fossil organism must be more closely related to one living group than to any other. Two living groups relevant in the case of the cornutes are the Echinodermata and Chordata. The view held here is that all of the cornutes are more closely related to living chordates than to living echinoderms.

Affinity with a particular living group can only be established on the basis of shared derived characters. Thus, all cornutes share with living chordates a locomotory tail, muscle blocks, and a notochord amongst other features (Jefferies 1986). But the features characterizing extant chordates did not all arise at once, that is, they did not all suddenly appear in the most recent

common ancestor of extant chordates. Rather, they were acquired gradually by the cornutes and inherited by the hypothetical common ancestor of all living chordates. This latest common ancestor of the living chordates, together with all of its descendants, constitute the crown-group Chordata.

There then remain those forms which do not belong to the crown-group Chordata, but which nevertheless are more closely related to this group than they are to echinoderms. These are the stem-group chordates (text-fig. 1). The total group of Jefferies (1986), or Hennig's (1969) 'Gesammtgruppe', in this case the phylum Chordata, consists of the stem-group chordates plus the crown-group chordates. All of the cornutes are stem-group chordates. The mitrates, not discussed in this paper, are primitive crown-group chordates.
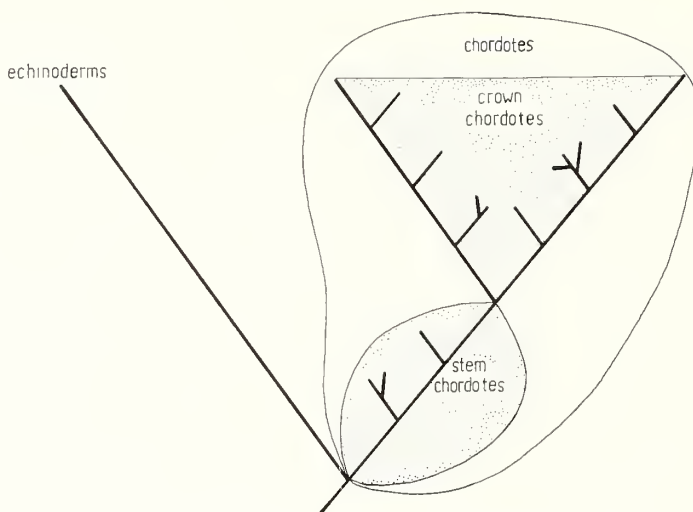
TEXT-FIG. 1. The stem-group concept as applied to chordates.

The problems arising in classifying fossils have been considered at length by Patterson and Rosen (1977), Wiley (1979, 1981), and Jefferies (1979, 1986). All these authors agree that the addition of a fossil species or group to an existing classification should be possible without disrupting that classification. Patterson and Rosen (1977) suggested that fossil groups be designated plesions and that 'it should no longer be necessary to rank fossils formally, except within extinct monophyletic groups' (p. 160). All of the taxa designated plesions in this work are stem-group chordates. This means that each plesion possesses at least one derived character which links it to the chordate crown-group.

In erecting a cladistic classification of the cornutes, Wiley's convention four (1979) has been adopted in placing certain groups 'sedis mutabilis' at the hierarchical level where their interrelations are known. Such groups form part of an unresolved trichotomy or polytomy. Jefferies (1986) has recently discussed the plesion concept and its usage. Under his definition, a plesion always includes a segment of the stem-lineage to which it is attached and consequently must always be paraphyletic. Moreover, if there is a trichotomy or polytomy in the stem lineage, all the groups involved are deemed to constitute a single plesion, since no member of this plesion can be shown to be more closely related to the crown-group than any other. The different approach of Jefferies from that of Wiley will not be considered further here and in fact would make no difference to the classification resulting from this work.

SYSTEMATIC PALAEONTOLOGY

Superphylum DEUTEROSTOMIA Grobben 1908
Subsuperphylum DEXIOTHETICA Jefferies 1979
Phylum CHORDATA Bateson 1886
Plesion (Family) SCOTIAECYSTIDAE Caster and Ubaghs, in Ubaghs 1967
Genus SCOTIAECYSTIS Caster, in Ubaghs 1967
Species *Scotiaecystis collapsa* sp. nov.

The trivial name *collapsa* refers to the fact that even the best specimens have collapsed upon burial.

Material, horizon, and localities. All the known specimens of *Scotiaecystis collapsa* sp. nov. are from the lower Cautleyan part of the Killey Bridge Formation, Ashgill Series (Upper Ordovician), near Pomeroy, Co. Tyrone, Northern Ireland. For an account of the stratigraphy see Mitchell (1977). According to R. P. Tripp (pers. comm. Oct. 1987), the upper part of the Killey Bridge Formation is of Rawtheyan age, but the evidence for this statement has not yet been published. The lower part of the Killey Bridge Formation remains of Cautleyan age. About 140 specimens of *S. collapsa* are known, all preserved as empty moulds and most of them disarticulated. Among the better specimens, E63072 carries part and counterpart of two almost complete individuals lying on top of each other, and of these, the individual nearer the camera in Plate 93, fig. 3 is chosen as holotype.

All the specimens are from Mitchell's localities 2 and 3 (1977, text-fig. 2), mostly from the latter. The details are as follows:

Locality 2. Warren Wood River. Grey shales on the banks and stream bed of the Warren Wood River, 2 km east-south-east from Pomeroy Square, 3·2 km south-south-west of Craigbardahessiagh, 160 m upstream of the junction with Bonn River (Irish grid reference H 7130 7128).

Locality 3. Little River. *In situ* in grey shales in a river cliff on the south bank of Little River and also from a small, old quarry tip, now largely removed, on the north bank of the river. 3·6 km east of Pomeroy Square, 1·6 km south-south-east of Craigbardahessiagh, 160 m east of Slate Quarry Bridge (H 7297 7268).

The material was collected in three small expeditions from the British Museum (Natural History). These took place in May 1977 (R. P. Tripp and S. F. Morris), in May 1978 (R. P. Tripp, S. F. Morris, and R. P. S. Jefferies), and in June 1984 (R. P. S. Jefferies and E. H. Westergaard). The first specimens of this species were noticed by Mr R. P. Tripp in August 1977 when breaking up material collected during May 1977. The specimens are all conserved in the Department of Palaeontology, British Museum (Natural History) with the following registration numbers:

Locality 2. E29662–E29681, E63088, E63089.
Locality 3. E29682–E29742, E63065–E63087 (including holotype on E63072), E63271–E63284.

METHODS OF STUDY

In order to reconstruct the three-dimensional shape of *S. collapsa* on the drawing-board, a life-size model was made using casts taken of the individual plates. To avoid any difficulties associated with scale, all plate impressions for the model, save one, were taken from the same specimen E29709*a*, *b* (part and counterpart). Plate l, which was missing on this specimen and which occupies a peripheral position, was taken from E29724*a*, *b*. The model was complete enough to give a precise idea of the general shape, but lacked plates g, j, r, h, and i. For these plates, impressions and latex casts taken from several other specimens were studied and they were reconstructed as accurately as possible.

Casts were made using Reprosil, a low-viscosity, high-precision silicone impression material. In making the model, the casts of individual plates were fixed to each other by a more viscous variant of the same substance in a different colour, so enabling the cement between the plates to be distinguished from casts of the plates themselves. This was applied around the plate junctions so that the integrity of the sutures was preserved. Any silicone left in the natural mould was easily removed with an organic solvent such as dichloromethane.

Many of the specimens were cleaned in thioglycollic acid (10 % in water) before latex casts were made using a red latex solution.

ANATOMICAL DESCRIPTION

Plate nomenclature follows that of Jefferies and Prokop (1972), as recently elaborated in Jefferies, Lewis, and Donovan (1987). A simple alphabetical notation is used. Plates given the same letter, initially on the basis of the crownward cornute *Reticulocarpos hanusi* Jefferies and Prokop, are believed to be homologous. Ubaghs, in his work on these animals, has used a different system for naming the plates. His notation is reproduced in Table 1 for comparison. The plates present in *S. collapsa* are labelled in text-fig. 2.

S. collapsa, like all other cornutes, consists of a distinct head and tail (Pl. 93, fig. 3; text-figs. 2, 3, 4, 5a). On the holotype the head is 13 mm across at its widest point. The whole animal, with straightened tail and including the length of the b-appendage, is about 30 mm long, though this length cannot be accurately determined. The head is asymmetrical and rather boot-shaped. It is bordered by a marginal frame of thirteen calcite plates, two of which (l and b) project from the frame, are greatly elongate, and can be called appendages. The tail is attached to the posterior part of the frame and is situated midway between the left and right sides of the animal.

Comparisons will be made, in particular, with *S. curvata* Bather (text-fig. 6) in the following description and character analysis. *S. curvata* is believed to be (for reasons discussed later) the

TABLE 1. Comparison of plate nomenclature and organ terminology according to Jefferies (1986) and Ubaghs (1970).

		Jefferies	Ubaghs
1. Plates		a	M_5
		b-appendage	glossale
		c-appendage	digitale
		d	M'_4
		e	M'_3
		f	M'_2
		g	M'_1
		h, i	adorales
		j	M_1
		k	M_2
		l-appendage	M_4, M_3
		m	zygale
		r	?
		s	M_4
		t	M_3
		u, ü	?
		v	M'_5
		w	M_6
		x	not distinguished from M_5
		y	central adoral
2. Organs		head	theca
		tail	aulacophore
		mouth	periproct
		anus	right adoral opening
		gills	cothurnopores, lamellipores
		notochord	water vascular canal
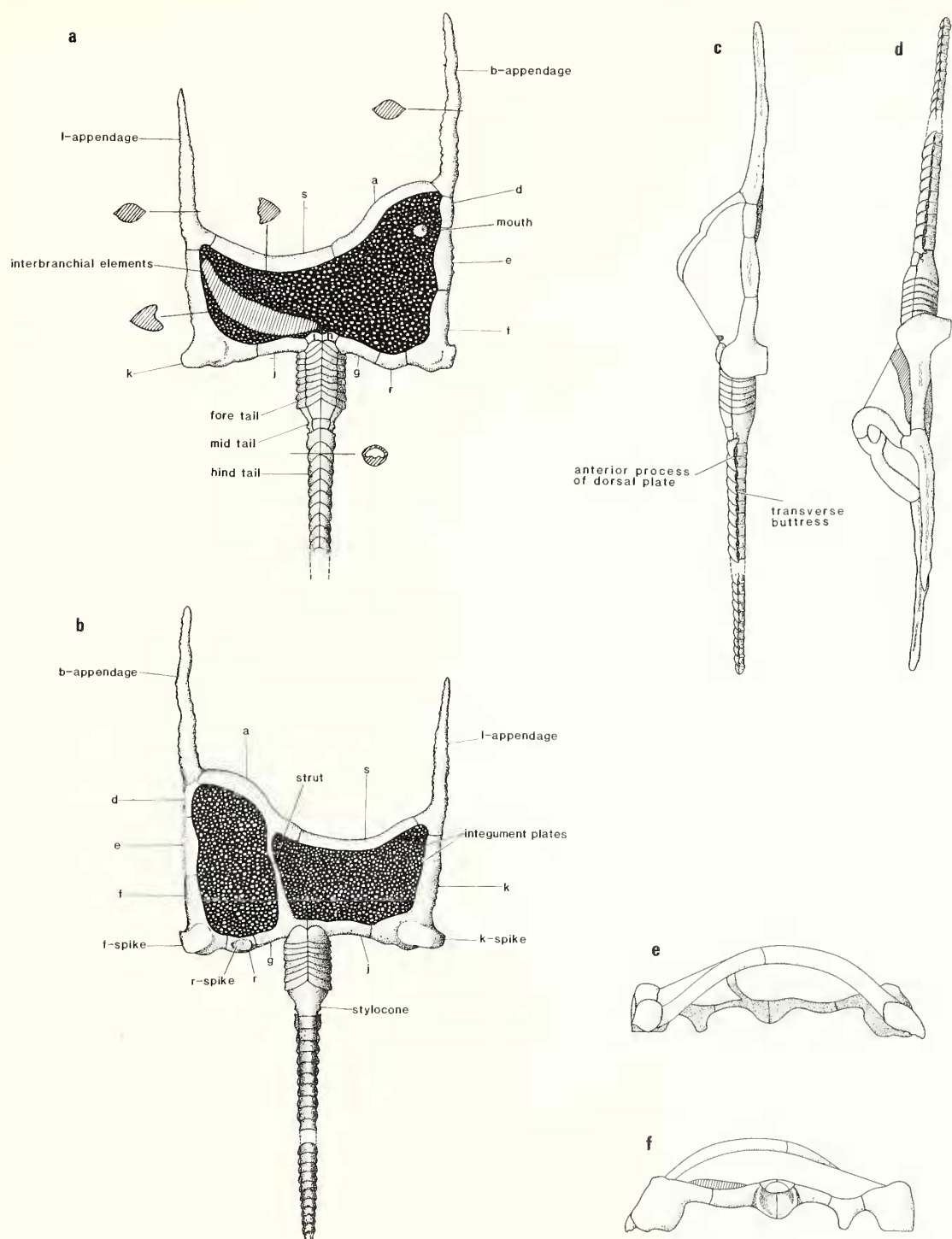
TEXT-FIG. 2. *Scotiaecystis collapsa. a*, dorsal aspect; *b*, ventral aspect; *c*, right lateral aspect; *d*, left lateral aspect; *e*, anterior aspect; *f*, posterior aspect.
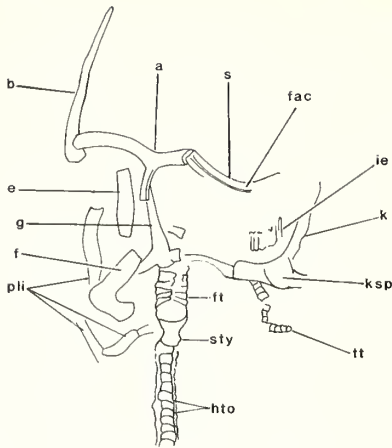
closest relative of the animal described here. The cornute *Cothurnocystis melchiori* Ubaghs, 1983, is, in the following description and discussion, referred to as *Thoralicystis melchiori*, for it is shown later that this species is a scotiaecystid and not closely related to other species of *Cothurnocystis*.
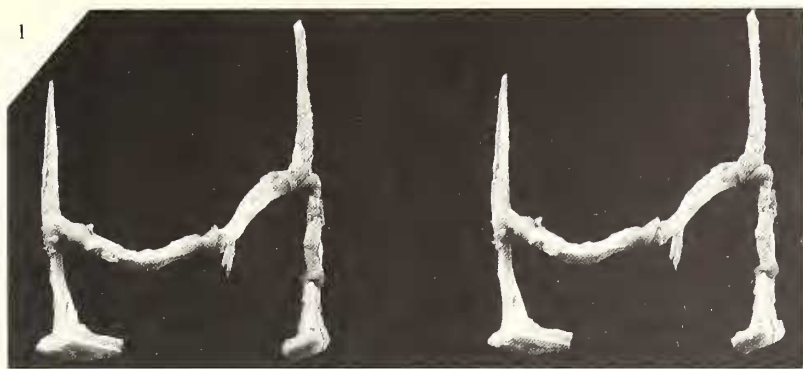
There is only one oral appendage in *S. Collapsa* as in some other scotiaecystids. This is thought to be plate b and equivalent to the left oral appendage of *C. elizae* Bather. However the b-appendage of *S. collapsa* is unique in two ways (text-fig. 7a): 1, running down each side of the plate are numerous serrations which appear slightly larger towards the base of the appendage, and 2, no less obvious are two kinks one about half-way along the plate, the other two-thirds of the way towards the rounded apex. These kinks are present on almost all specimens where there is a mould of the b-appendage. The left appendage or plate l (spinale of Ubaghs) is similarly serrated and both b and l are dorsoventrally compressed, presumably helping these appendages to slice through the substrate during locomotion, like a pair of bread knives. Their action would create a cloud of suspended mud particles which could be sucked in through the mouth for feeding. Plate l, unlike b, terminates in a point (text-fig. 7d).

Plate s, another scotiaecystid feature, is also found in *S. collapsa*. This plate is markedly curved and together with plate a is responsible for the dorsally convex shape of the anterior frame (Pl. 93, fig. 2; text-fig. 2e, f). This feature differs only slightly from that of *S. curvata*, in that the summit of the convexity is not at the s–a junction but on plate s. The functional significance of such an arcuate shape is hard to explain, particularly as the posterior frame is not nearly as convex. Interestingly, in one specimen (E29681) plate s is unusually long relative to the other plates and very slender. This specimen was presumably juvenile in view of its small size. In growing to its adult condition, s would have lengthened relatively less than the other plates.

Three protuberances are found attached to the frame on the ventral surface of the head which

PLATE 93

CRIPPS, *Scotiaecystis collapsa* sp. nov.

are extremely variable in shape and size. These spike-like processes are found on plates f, k, and r, and are named after the plates that bear them. The f- and k-spikes also have significant laterally directed projections which are not found in *S. curvata*. On plate k the lateral and ventral processes are connected by a flange, whereas the lateral process on f terminates very abruptly with a pointed anterior edge. The r-spike is the most variable of all, but commonly is a finger-like projection, ovoid in cross-section and directed away from plate f. These spikes probably served to anchor the head in the mud, preventing it from slipping forwards during locomotion (Jefferies *et al.* 1987). Plate k, like b and l, is serrated along part of its left edge.

Although plate a is slightly shorter relative to s, it is of the same general appearance as its homologue in *S. curvata*. It sends a ventral process, a part of the strut, which may have possessed a slight kink, to meet plate g and support the ventral integument. Plate e, like k, b, and l, is serrated. The serrations are, as elsewhere, arranged in a line, but are found only upon the outer edge of the plate. They are fewer and larger than those of the other plates. Four serrations were counted. Neither e nor k is serrated in *S. curvata*.

The small plates h and i, near the tail-base, show important differences from those in *S. curvata*. This region, where the fore tail joins the head, is the most complicated part of the animal (text-figs. 7*b*, 8, 9). Both h and i have a strongly convex anterior face and a concave posterior face, thus distinguishing them from their homologues in *S. curvata* which are almost square in dorsal aspect. Furthermore, in *S. collapsa*, unlike *S. curvata*, h and i do not send out ventral processes to meet in the mid-line anterior to the posterior coelom (text-fig. 9*c*), and i is not in contact with the interbranchial elements.
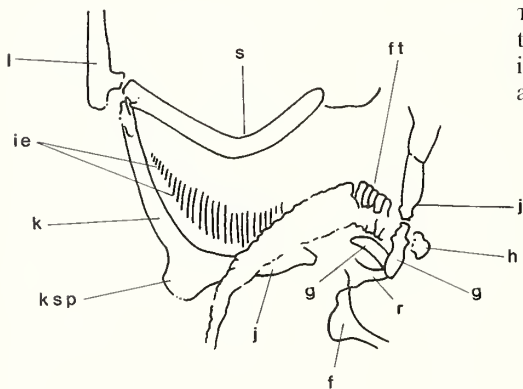
TEXT-FIG. 4. Outline drawing of text-fig. 5*a*. Labels other than plate notation are; ft, fore tail of upper animal; ie, interbranchial elements; ksp, k-spike. The two individuals are lying approximately at right angles to eaeh other.

Plates g and j meet ventrally at the tail-base (text-fig. 7*b*). Dorsally, these two plates have curved facets for the attachment of h and i (text-fig. 9*b*). On the posterior surface of g and j in the region of the mid-line is a symmetrical basin (text-fig. 2*f*). This excavation is believed to have carried the brain. Also observed here, and appearing to leave the brain, are two canals for the median-line nerves. Lateral to these canals are the so-called pyriform bodies which, like the nerve canals, are preserved as natural casts (text-fig. 8). These bodies have been interpreted by Jefferies (1968) as the trigeminal ganglia and seem to overlap the reception groove for the fore tail anteriorly (text-figs. 8 and 9).

Plates g, j, and the small plate d exhibit no important differences from the same plates in *S. curvata*. All the marginal plates are approximately triangular in cross-section (text-fig. 2*a*), except for the appendages, and the latexes show that they were made of labyrinthic stereom (Smith 1984). Appendage l, unlike all the other plates (including b), was constructed from a fasciculate type of stereom.
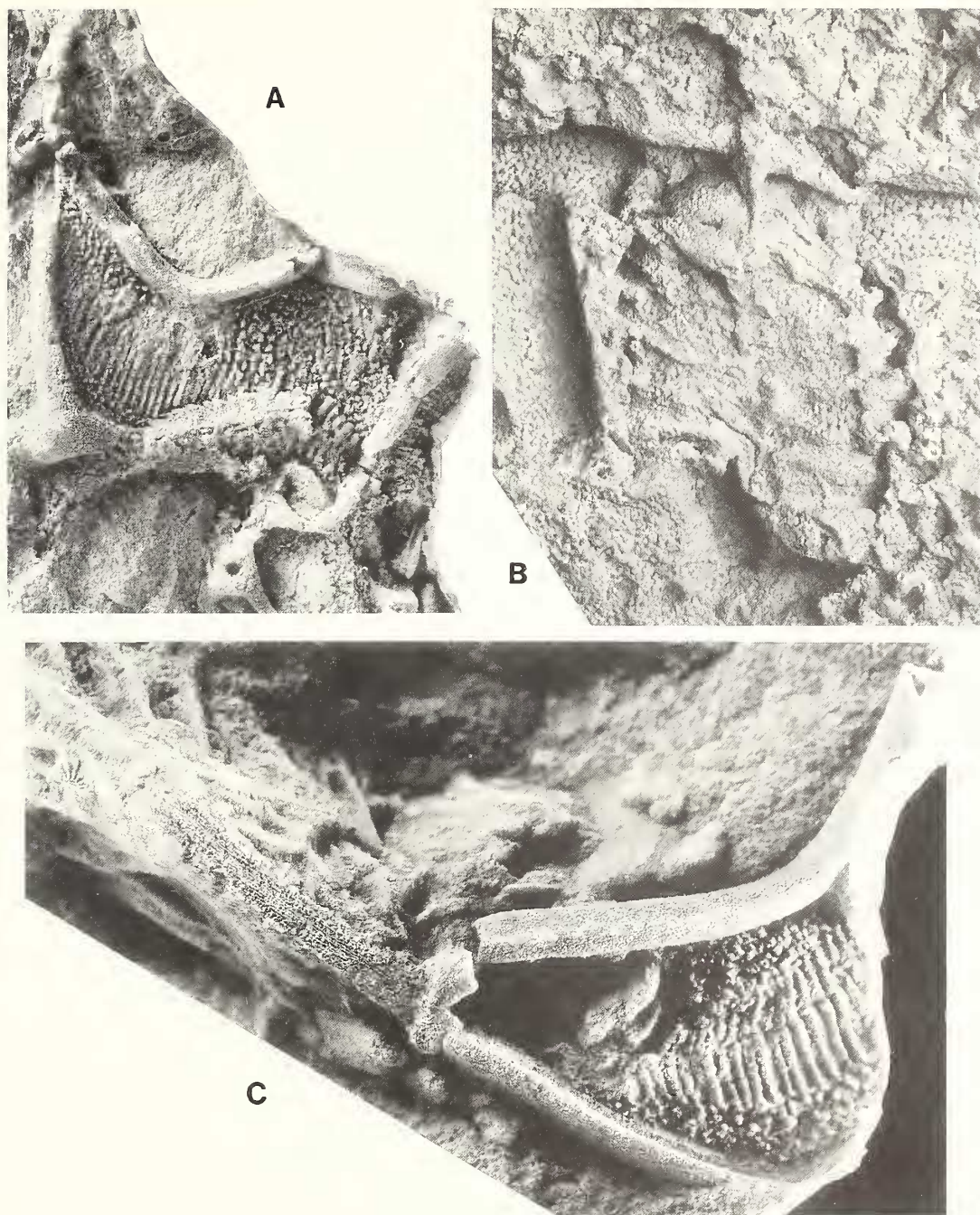
TEXT-FIG. 5. *Scotiaecystis collapsa* sp. nov. A, latex cast of BMNH E63072*b* showing two individuals, one lying on top of the other, of which the lower individual is the holotype in dorsal aspect (text-fig. 4). Most of the head of the upper individual is missing but the posterior frame is present, ×5·1. B, natural mould, BMNH E63072*b*, SEM close-up of fore tail and cerebral basin, ×26·6 (text-fig. 8). C, latex of BMNH E29683*a* lit from the bottom right in order to show more clearly the interbranchial elements as well as plates l, k and s, ×7·3.
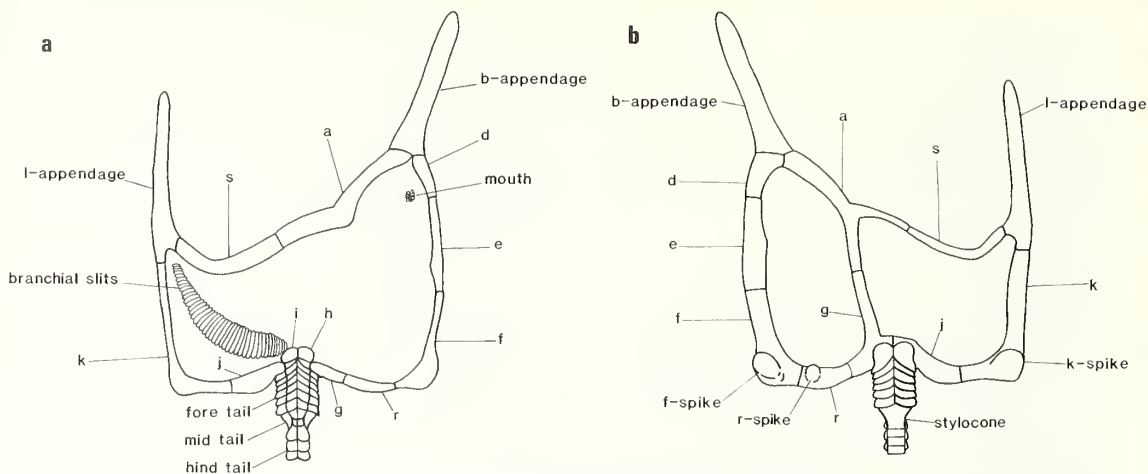
TEXT-FIG. 6. *Scotiaecystis curvata.* a, dorsal aspect; b, *Scotiaecystis curvata*; ventral aspect. Redrawn after Jefferies 1986, text-figs. 7.12a and 7.12c, respectively.

HEAD OPENINGS AND INTERBRANCHIAL ELEMENTS

The interbranchial skeletal elements of the gill openings, which number about forty-five (an accurate count is not possible), are arranged in a curved series and situated in the left part of the dorsal integument. They are placed more posteriorly than in *S. curvata*. If the shape of the animal is compared with a boot, then the gills occupy the posterior half of the 'toe' (text-fig. 10). In other words, the series of gills does not neatly bisect this area (the left part of the dorsal integument), unlike the gill series in *S. curvata* and *T. zagoraensis* (Chauvel). This relatively posterior position of the gills is probably the primitive condition within the cornutes (see below). Unlike *S. curvata*, the interbranchial plates are not chevron-shaped and in fact are slightly concave dorsally (text-fig. 11). They are altogether much simpler structures than those of *S. curvata*, possessing none of the grooves or more complicated processes of the latter and lying more or less parallel to each other (text-fig. 5c). Ventrally, the elements bear relatively simple terminal processes (text-fig. 11b). Another interesting feature of the interbranchial elements is that, on one specimen (E29683), a suture is visible running across some of the plates and found about one-quarter of the way down each element from the front edge. If, as Jefferies believes, these plates represent the fusion of adjacent halves of anterior and posterior u-plates, then these sutures are well placed to be the vestiges of such a transformation.

The only evidence of the mouth is found on specimen E63072a in the form of a few pointed, elongate plates which are largely hidden beneath a displaced e-plate. Nevertheless, these plates are enough to show that the mouth is dorsally placed as in all known scotiaecystids, except *T. zagoraensis* as described and figured by Chauvel (1971). In both *S. collapsa* and *S. curvata* there is no sign of an external gonopore-anus and the gonorectal canal opens into the gills. This canal is preserved as a natural cast on E63072b (text-figs. 5b and 8). It is a much larger structure than in *S. curvata* and runs through the i–j suture on its way to the gill slits (text-fig. 9c).

CHAMBERS AND SOFT ANATOMY OF THE HEAD

The asymmetrical shape of most cornutes, including *S. collapsa*, has been explained by Jefferies (1979) as a consequence of descent from a bilaterally symmetrical ancestor that lay down on its right side. The arguments supporting this view will not be repeated here, but Jefferies (1986)
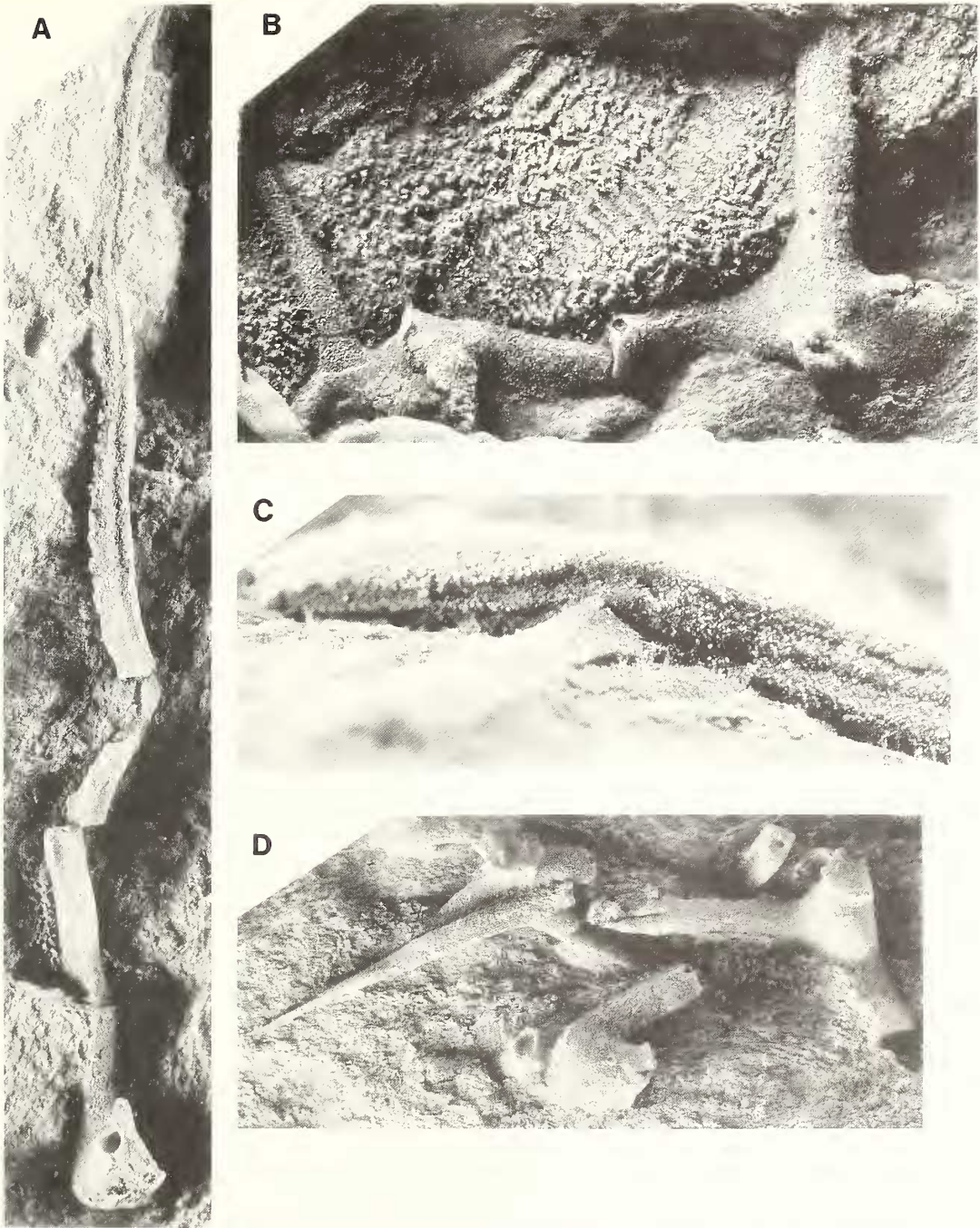
TEXT-FIG. 7. *Scotiaecystis collapsa* sp. nov. A, latex of BMNH E29682*b* showing plates f, e, d, and b in ventral aspect. The serrations on the b-appendage can be clearly seen, ×6·5. B, latex of BMNH E29682*a* showing the g–j junction, plate k and, faintly, some of the interbranchial elements, ×8·8 (text-fig. 9*c*). C, latex of BMNH E29706 viewing the inner surface of plate a and showing the lines of attachment of the buccal cavity and pharynx, ×13·8 (text-fig. 12). D, latex of BMNH E29715*a* showing the l-appendage (top), plate k beneath it, and plate f left of centre, ×4·8.
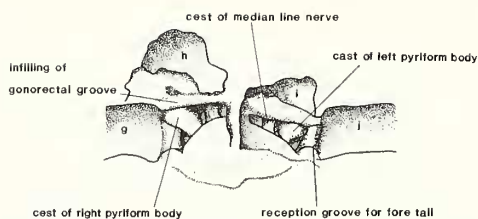
TEXT-FIG. 8. *Scotiaecystis collapsa*. Tail-base region of natural mould (E63072b).
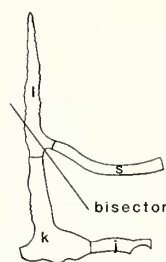
TEXT-FIG. 10. *Scotiaecystis collapsa*. Bisector of 'toe' region.

TEXT-FIG. 11. *Scotiaecystis collapsa*. Interbranchial elements: *a*, external; *b*, lateral; *c*, internal views.

TEXT-FIG. 9. *Scotiaecystis collapsa*. *a*, reconstruction of tail-base region; *b*, tail-base region with h and i removed; *c*, anterior view of tail-base region.

provides a synthesis of the evidence. This hypothetical ancestor would most likely have been similar to the living hemichordate *Cephalodiscus* resting upon its right side—an orientation called dexiothetism. Such an ancestor, Jefferies believes, also gave rise to the echinoderms. Therefore the two phyla Echinodermata and Chordata have been united by him to form the superphylum

TEXT-FIG. 12. *Scotiaecystis collapsa*. Inner face of plate *a*, BMNH E29706, text-fig. 7*c*.
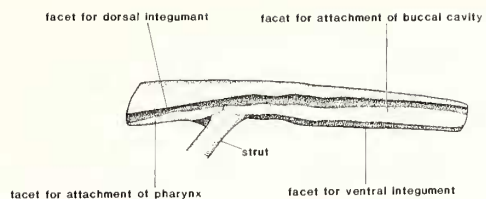
Dexiothetica. Jefferies' theory is uniquely able to account for the peculiar asymmetries observed in the development of echinoderms, tunicates, and cephalochordates. It also explains the boot-like shape so characteristic of many primitive cornutes.

In the cornutes there is evidence for the existence of four chambers in the head; the buccal cavity just behind (in some cases below) the mouth, the pharynx situated in the 'toe' part of the 'boot', the posterior coelom just anterior to the tail base, and the right anterior coelom underlying the pharynx. A fifth chamber is postulated to exist based upon comparative evidence alone. This is the left anterior coelom and is reasoned to be present through a comparison with *Cephalodiscus*. Such a comparison suggests that the right metacoel of *Cephalodiscus* is the homologous chamber of the right anterior coelom of cornutes.

The evidence for the existence of the head chambers in *S. collapsa* is described below and shown in text-figs. 12 and 13. The buccal cavity, pharynx, and posterior coelom have all left evidence of
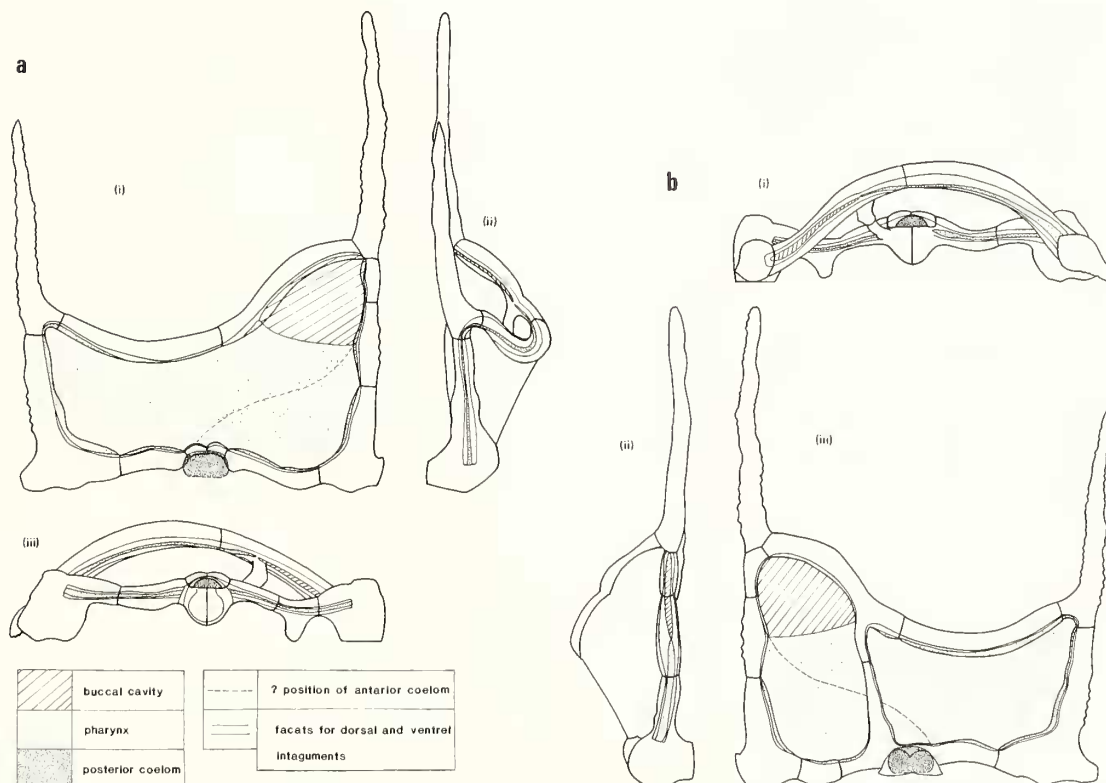
TEXT-FIG. 13. *Scotiaecystis collapsa*. *a*, Reconstruction of internal cavities of head: i, dorsal; ii, left lateral; iii, posterior aspects. *b*, reconstruction of internal cavities of head (for key see text-fig. 13*a*): i, anterior; ii, right lateral; iii, ventral aspects.

their presence in the form of a series of ridges and grooves which can be seen on the inner faces of the marginal plates (text-figs. 7c and 12). In addition to these clues, the gross morphology of a given region of the head can indicate the position of a chamber. The only good example of this is in the case of the buccal cavity, with the shape and position of plates a and e enabling recognition of its posterior boundary. This evidence is backed up by other clues which come from studying the inner surfaces of the plates concerned (text-figs. 12 and 13).

On the inner faces of the marginal plates are found an upper, a middle, and a lower zone. The upper and lower zones are concave excavations whilst the middle zone is a distinct ridge. The height of this ridge, and the degree of separation of the upper and lower zones varies from place to place. The upper and lower zones are concave facets for the attachment of dorsal and ventral integuments, respectively. The middle zone represents the attachment of various head chambers to the marginal frame. A clearly defined facet, also concave, can be found on both lateral surfaces of the ventral strut which is formed by plates a and g. These facets are for the attachment of the ventral integument alone.

The pharynx would have been the largest chamber in the head, occupying about two-thirds of the space available. Its existence is confirmed by the presence of grooves on the inner surfaces of the head plates. There is no observable boundary between the pharynx and the right anterior coelom in S. collapsa, but grossly they probably had the same relative positions as in all other cornutes for the following reasons: 1, the gill slits are in the left part of the dorsal integument and would have opened out of the pharynx; 2, the gonorectal groove emerges from the presumed position of the right anterior coelom and indicates that the gonad and most of the non-pharyngeal gut were in the 'heel' part of the head; and 3, the height of the frame is greater to the right of the tail than to the left of it, so this part of the animal was capacious enough to hold the right anterior coelom and its contents.

The anterior border of the posterior coelom is marked by a groove in the natural mould of E63072b corresponding to a ridge on plates g and j. This chamber, which is roofed over by plates h and i, probably extended posteriorly as far as the fore tail. The left anterior coelom, in all cornutes and mitrates, is purely hypothetical and virtual.

TEXT-FIG. 14. *Scotiaecystis collapsa.* Integument plates.

The integument plates are bobbin-shaped as in *S. curvata.* However, the axis of the bobbin is more elongate and sometimes lacks one of the two heads—usually the outer one (text-fig. 14). Plate density, i.e. number of plates per unit area, is greater on the ventral than dorsal surface, and, on the dorsal surface, between the area surrounding the gills. The density variations are thus similar to those in *S. curvata.*

THE TAIL

The tail of *S. collapsa* is represented on about twelve specimens but is most complete on E63072a and b (Pl. 93, figs. 3 and 4). On E63072a the tail is seen in ventral aspect on two individuals. It is clearly divided into fore tail, mid tail, and hind tail. Although an accurate count of the number of hind tail segments is not possible, it is fairly certain that there are at least twenty-one segments, which is more than have so far been discovered in *S. curvata* (Jefferies 1968, p. 275, states that the hind tail of *S. curvata* must have had about sixteen segments).

The fore tail is composed of eight segments. The skeleton of each segment consists of a pair of small dorsal plates and a pair of much larger ventral plates. The ventral plates are somewhat wider

TEXT-FIG. 15. *Scotiaecystis collapsa.* Stylocone; internal structure in dorsal aspect.
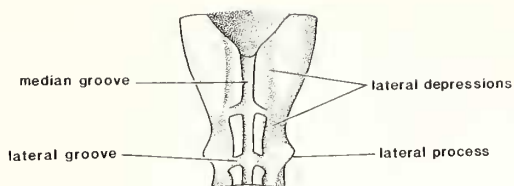
than the dorsal plates (meaning width in a direction transverse to the long axis of the tail) and hence are visible in dorsal as well as ventral aspect. The plates of each segment imbricate beneath those of the segment immediately in front. This is probably an adaptation allowing for dorsoventral flexibility of the fore tail, since when the tail is stretched during flexion the plates are able to slide over each other without stretching the intervening soft tissues. The most anterior pair of ventral plates overlap plates g and j.

The fore tail segments terminate posteriorly at the stylocone. This is a funnel-shaped structure, overlain dorsally by two pairs of plates which are very different in shape to those found anywhere else in the tail. In form they are much like the corresponding plates in *S. curvata.* The stylocone itself is more ventrally situated than in most species and on many specimens is seen to bear a pair of laterally directed processes which are like those observed by Ubaghs (1983) in *T. melchiori,* although in the latter they are directed upwards.

Several specimens also show the internal structure of the stylocone in dorsal aspect (Pl. 93, fig. 5; text-fig. 15). There is a median groove, believed to have carried the notochord, which is always preserved as a natural cast. The soft structure which it housed must have extended into the fore and hind tails. The median groove sends out two pairs of lateral grooves which are directed slightly rearwards. These grooves disappear underneath a shelf on either side. Some detail can be seen upon this shelf too in the form of a pair of depressions. The posterior depression borders the bases of the above-mentioned lateral processes, whilst the anterior one runs towards the front edge of the stylocone. Similar depressed areas have been described by Ubaghs (1970) in the stylocones of *Cothurnocystis primaeva* Thoral and *T. griffei* (Ubaghs).

The hind tail, as stated earlier, consists of at least twenty-one segments. As in the mid and fore tail, the dorsal plates are paired and meet at the mid-line. There is only one ventral ossicle per segment, however, as is true of most cornutes. The ventral ossicles approximate to hemicylinders but gradually become less deep distally. Concomitant with this distalward flattening are two further changes: 1, the sutures between the ossicles change from being planar and straight in ventral aspect to being curved and convex anteriorly in ventral aspect; 2, each ossicle bears upon its dorsal face a pair of transverse buttresses. As the ossicles flatten so these buttresses become more laterally orientated (text-fig. 2c, d) and hence visible in ventral view.

Small, rounded protuberances appear on the ventral surfaces of the ossicles towards the tail end (text-fig. 2b). There is one to each ossicle and they are situated in the mid-line, close to the posterior suture. These were most likely used for gaining a good purchase on the substrate when the animal used its tail like a hook during the locomotory cycle (see discussion of locomotion in Jefferies *et al.* 1987). These knobs are clearly seen on the last seven ossicles in E63072a and may well be homologous with the ventral spikes seen in more crownward cornutes such as *Reticulocarpos hanusi.* The terminal tail ossicle of the lower individual on specimen E63072a has a rounded tip. A similar condition has been described in *T. melchiori* (Ubaghs 1983, p. 35, text-fig. 7c and pl. VIII, fig. 1). The situation in these two species therefore contradicts Jefferies's assertion that autotomy at the end of the cornute tail was 'normal in cornute ontogeny' (1986, p. 230). It appears, however, to have been habitual in mitrates and in the most crownward cornutes such as *R. hanusi,* for this species is sometimes observed to have only one ossicle in the hind tail and has never been shown to have more than four (Jefferies and Prokop 1972). The tail impression of the lower individual on specimen E63072a also demonstrates that the hind tail was flexible in the horizontal plane (Pl. 93, fig. 3; text-fig. 3).

The dorsal surfaces of the hind tail ossicles are not well shown in any specimen and nothing can be said concerning the facets for articulation of the dorsal plates. A longitudinal median groove can be recognized, as in the stylocone, with a pair of oblique, rearwardly directed lateral grooves in each ossicle. The dorsal plates of the hind tail are hemicrescentic in outline (text-fig. 2*a*) when viewed from above. Apart from the first pair of plates, which bear small, forward-facing processes, these plates are uniform except that (like the ventral hind tail ossicles) they narrow gradually towards the end of the tail. The oddest aspect of the whole hind tail is that each dorsal plate makes contact with three ventral ossicles, i.e. it extends along the whole length of one ossicle and projects anteriorly on to the more proximal neighbouring ossicle and posteriorly on to the more distal neighbouring ossicle. Posteriorly, each plate overlaps the plate behind it. Each plate bears a large anterior process which lies just in front of the transverse buttress belonging to one of the ossicles. The plate extends posteriorly, overlapping the following plate, traversing an entire ossicle (text-fig. 2*c, d*). In *S. curvata*, by contrast, each plate is in contact with only a single ossicle.

INTERRELATIONS OF STEM-GROUP CHORDATES

Twenty-one species of cornutes were coded for thirty-nine characters and subjected to a cladistic analysis using PAUP (version 2.4.1), a computer program devised by Dr David Swofford of the Illinois Natural History Survey. PAUP (Phylogenetic Analysis Using Parsimony) has a number of option settings. No weights were applied to any of the characters and *Ceratocystis perneri* Jaekel was used to root the tree. *C. perneri* is the only cornute to retain a hydropore and is considered by Jefferies (1969, 1979, 1986), on the basis of this and other characters, to be the most primitive known chordate. PAUP is able to deal with missing data, represented in the data matrix (Table 2) by a question mark, which is treated as either 0 or 1, and reversals of character-state are permitted.

The program produced an initial tree and then undertook global branch swapping until a shorter tree was found. PAUP discovered three trees with a minimum length of sixty-nine steps and with a consistency index of 0·565. From these trees an Adams's consensus tree (Adams 1972) was constructed (text-fig. 16) which provides a summary of the different most parsimonious solutions. The trichotomy consisting of *Amygdalotheca griffei* Ubaghs, *R. hanusi* and *R. pissotensis* Chauvel can be resolved through the addition of primitive crown-chordates (mitrates) to the tree (text-fig. 17). *R. pissotensis* is the most crownward cornute species, sharing with the mitrates a convex ventral surface (in other cornutes it is the dorsal surface which tends to be convex). *Galliaecystis lignieresi* Ubaghs was placed by Jefferies (1986) in a more crownward position than shown in text-figs. 16 and 17, due its possession of a dorsal bar. But set against this, *Galliaecystis* retains an l-appendage, an asymmetrical head, and a large number of gill openings. It seems more parsimonious to assume that *Galliaecystis* acquired its dorsal bar independently of *Reticulocarpos*.

Phyllocystis and *Chauvelicystis* form a clade on the basis of five synapomorphies. However, of these five only one—tuberculated posterior marginals—is uniquely derived. In *Chauvelicystis* the tubercles articulate with the more posterior spines characteristic of this genus. The two species of *Phyllocystis*—*P. blayaci* Thoral and *P. crassimarginata* Thoral—appear to form a clade, both having a heart-shaped marginal frame.

The monophyly of the Scotiaecystidae (text-fig. 18) is supported by two uniquely derived characters. These are the possession of plate s and of interbranchial elements. The relations within this group are more problematical. The relative positions of *T. griffei* and *T. melchiori* are uncertain. On the one hand the two species may be sister taxa as shown in the consensus tree. This hypothesis is based upon the possible reappearance in these species of one of the two small plates (v or w) at the anterior edge of the head. But, as discussed below, it is not possible to know whether one, both, or neither of these plates was present in the most primitive scotiaecystid, *T. zagoraensis*. If both were absent then the reappearance of one of them (v or w?) in *T. griffei* and *T. melchiori* is a possible synapomorphy. *T. griffei* also shares loss of the e-spike with more derived scotiaecystids, but once again the condition in *T. zagoraensis* is unknown.

TABLE 2. Character data matrix for twenty-one species of stem-group chordates. Character-states described represent the derived conditions.

Taxa (columns 1–21):
1 = *Ceratocystis perneri*; 2 = *Nevadaecystis americana*; 3 = *Protocystites menevensis*; 4 = *Cothurnocystis primaeva*; 5 = *C. fellinensis*; 6 = *C. courtessolei*; 7 = *C. elizae*; 8 = *Thoralicystis melchiori*; 9 = *T. zagoraensis*; 10 = *T. griffei*; 11 = *Bohemiaecystis bouceki*; 12 = *Scotiaecystis curvata*; 13 = *S. collapsa*; 14 = *Galliaecystis lignieresi*; 15 = *Amygdalotheca griffei*; 16 = *Reticulocarpos hanusi*; 17 = *R. pissotensis*; 18 = *Phyllocystis blayaci*; 19 = *P. crassimarginata*; 20 = *Chauvelicystis spinosa*; 21 = *C. ubaghsi*.

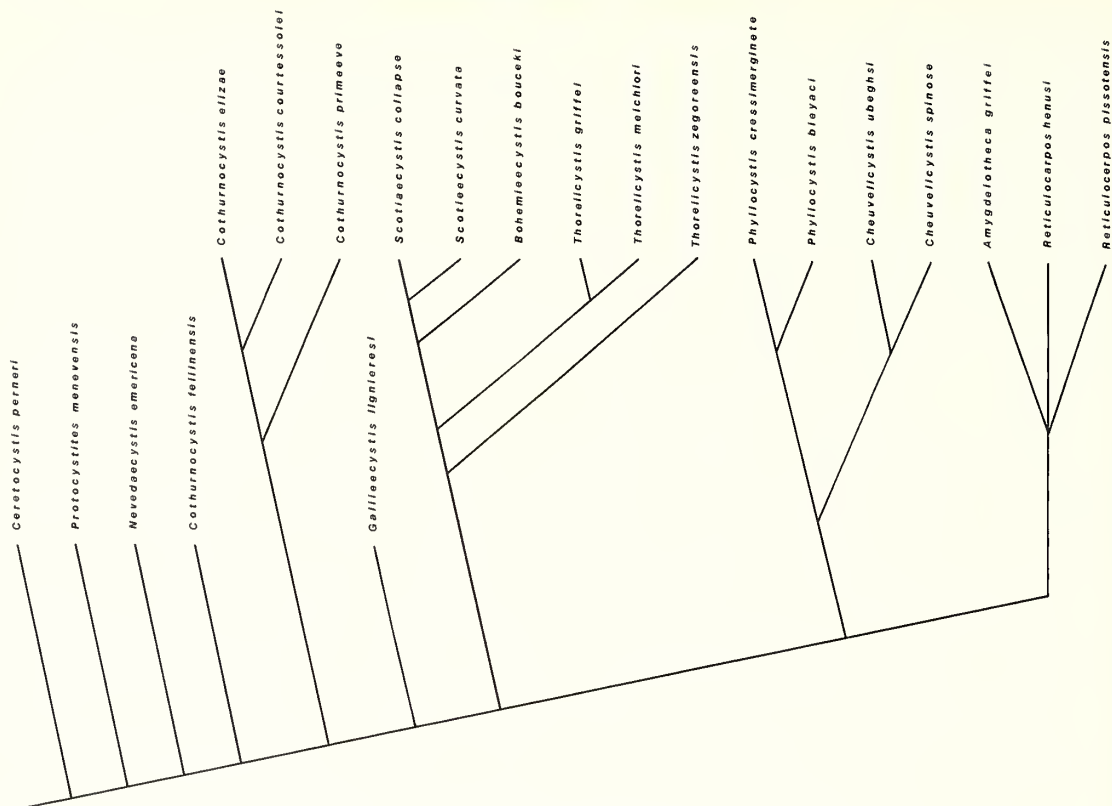| Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Absence of l-appendage	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Tuberculated posterior marginals	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?
Heart-shaped head	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Head bears fringe of spines	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Peripheral flange	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	0	0
Fore-tail plates suture in dorsal midline	0	?	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?
Hind tail bearing ventral processes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	?	?
Absence of i-k contact	0	0	1	0	0	0	?	?	0	0	1	0	0	0	0	0	0	0	0	1	?
Absence of u and ŭ	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Gills divide 'toe' into two equal halves	0	0	0	?	?	?	0	0	1	0	0	1	0	?	0	0	0	0	0	0	0
Anterior frame dorsally convex	0	0	0	0	0	0	0	?	?	?	0	1	1	1	0	0	0	0	0	?	?
Rounded integument plates cover pharynx	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1	0	0	0	1
Large number of gill openings	0	0	0	?	?	?	1	1	1	1	1	1	1	?	0	1	1	0	0	0	0
Symmetry	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anterior u-plates	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dorsal bar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plate a excluded from strut	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Branchial plates convex dorsally	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0
Interbranchial elements	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0
Plate r	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Absence of median eye	0	0	0	?	0	?	1	1	1	1	1	1	1	1	1	1	1	0	0	0	?
c-d articulation	0	?	0	1	0	1	1	?	?	0	0	0	0	0	0	0	0	0	0	0	0
Gonorectal canal opens into gills	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0
Gonopore-anus opens to left of tail	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dorsal mouth	0	0	0	0	?	0	0	1	1	1	1	0	0	1	0	0	0	1	1	?	?
Ventral strut	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Forward shift of buccal cavity on to plate d	0	0	0	0	?	1	0	1	?	?	1	0	0	1	1	?	?	1	1	1	1
Absence of c	0	?	0	0	0	0	0	0	?	0	0	0	0	1	0	1	?	?	?	0	?
Absence of v and w	0	?	0	0	0	0	0	0	?	0	0	0	0	1	?	1	1	?	?	1	1
Absence of v or w	0	?	0	0	0	0	0	?	?	0	0	0	0	1	?	1	1	1	1	1	1
Absence of e-spike	0	0	0	0	0	1	1	0	?	1	1	0	1	1	1	1	1	1	1	1	1
Absence of y	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Absence of x	0	1	0	0	0	0	0	0	?	?	1	1	1	1	1	1	1	0	0	0	0
Plate s	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Plate t	0	0	0	0	?	1	1	0	0	0	1	0	0	1	0	1	1	0	0	1	0
Absence of f and k spikes	0	0	0	0	0	0	?	0	?	0	1	0	0	1	1	1	1	1	1	1	1
Flexible head floor	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Flexible head roof	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Absence of hydropore	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

TABLE 2. Character data matrix for twenty-one species of stem-group chordates. Character-states described represent the derived conditions.

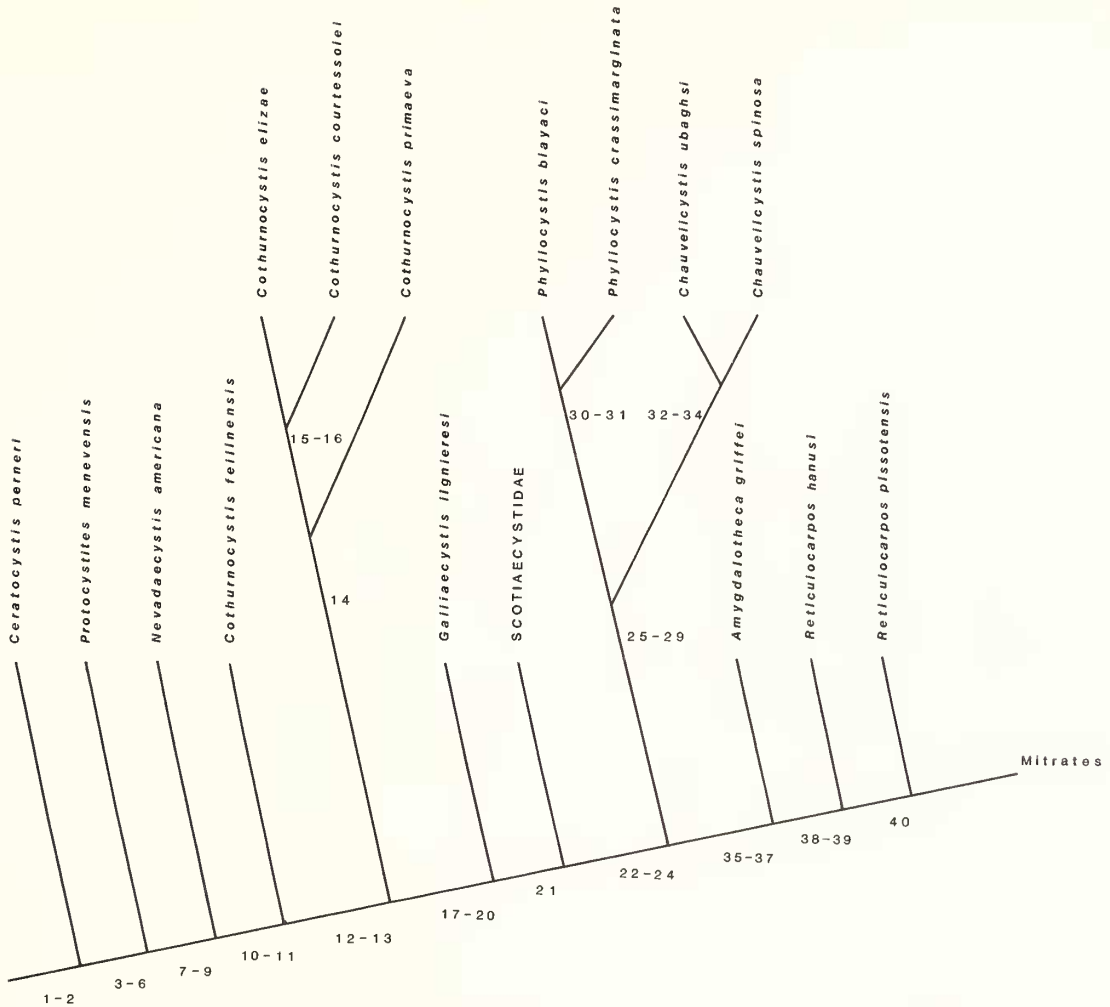| Taxa	Absence of hydropore	Flexible head roof	Flexible head floor	Absence of f and k spikes	Plate t	Plate s	Absence of x	Absence of y	Absence of e-spike	Absence of v or w	Absence of v and w	Absence of c	Forward shift of buccal cavity on to plate d	Ventral strut	Dorsal mouth	Gonopore-anus opens to left of tail	Gonorectal canal opens into gills	c-d articulation	Absence of median eye	Plate r	Interbranchial elements	Branchial plates convex dorsally	Plate a excluded from strut	Dorsal bar	Anterior u-plates	Symmetry	Large number of gill openings	Rounded integument plates cover pharynx	Anterior frame dorsally convex	Gills divide 'toe' into two equal halves	Absence of u and ü	Absence of r-k contact	Hind tail bearing ventral processes	Fore-tail plates suture in dorsal midline	Peripheral flange	Head bears fringe of spines	Heart-shaped head	Tuberculated posterior marginals	Absence of l-appendage
Ceratocystis perneri	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nevadaecystis americana	1	1	0	0	0	0	0	0	0	?	?	?	0	1	0	1	0	?	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	0
Protocystites menevensis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cothurnocystis primaeva	1	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	?	0	0	0	0	0	1	0	?	0	0	?	1	0	0	1	0	0	0	0	0
C. fellmensis	1	1	1	0	1	0	0	0	0	0	0	0	?	1	?	1	0	0	0	0	0	0	0	0	1	0	?	0	0	?	1	0	0	1	0	0	0	0	0
C. courtessolei	1	1	1	0	1	0	0	1	1	0	0	0	1	1	0	1	0	1	?	0	0	0	0	0	1	0	?	1	0	?	1	?	0	1	0	0	0	0	0
C. elizae	1	1	1	0	1	0	1	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Thoralicystis melchiori	1	1	1	0	0	1	0	1	0	1	0	0	1	1	1	1	0	?	1	0	1	0	0	0	0	1	0	?	0	?	0	1	G	1	0	0	0	0	0
T. zagoraensis	1	1	1	?	0	1	?	1	?	?	?	?	1	0	0	?	1	0	1	0	1	0	0	0	0	1	0	?	1	1	1	0	0	0	0	0	0	0	0
T. griffei	1	1	1	0	0	1	1	1	1	0	0	1	1	1	1	0	1	0	1	0	1	0	0	1	0	1	0	?	0	1	1	1	0	1	0	0	0	0	0
Bohemiaecystis bouceki	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Scotiaecystis curvata	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0
S. collapsa	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0
Galliaecystis lignieresi	1	1	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	1	1	0	?	0	1	?	1	1	1	0	0	0	0	0	0	0
Amygdalotheca griffei	1	1	1	1	0	0	1	1	1	?	?	0	1	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	1
Reticulocarpos hanusi	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	1
R. pissotensis	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	?	0	0	0	1
Phyllocystis blayaci	1	1	1	1	1	0	1	0	1	0	1	?	?	?	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	1	1
P. crassimarginata	1	1	1	1	0	1	0	1	0	1	?	?	?	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1
Chauvelicystis spinosa	1	1	1	1	1	0	0	0	0	1	1	0	1	1	?	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	?	0	1	1	?	?	0	1	1
C. ubaghsi	1	1	1	1	1	0	0	0	0	1	1	0	1	1	?	1	0	0	?	0	0	0	0	0	1	0	1	0	0	0	?	0	1	?	?	?	0	1	0

TEXT-FIG. 16. Consensus tree for stem-group chordates.

Cothurnocystis primaeva possesses a confusing array of plesiomorphic and apomorphic traits, but a clue to its systematic position may lie with the contact that the c-appendage makes with plate d. In *C. elizae* and *C. courtessolei* Ubaghs this contact is in the form of a mobile articulation (albeit more obviously so in *C. elizae*). The extent of its development in *C. primaeva* is unclear from published photographs (Ubaghs 1970). However, in the same paper Ubaghs states that the c-appendage (his digitale) is attached to plate d (his M'4) 'par une articulation qui paraît peu différenciée'. It is therefore possible that this character, the c–d articulation, defines a group consisting of *C. elizae*, *C. courtessolei*, and *C. primaeva*. Within this group *C. elizae* and *C. courtessolei* share a plate t (acquired in parallel with the *Phyllocystis-Chauvelicystis* clade) and a covering of circular integument plates for the pharynx.

The cladogram presented in text-fig. 17 is the most parsimonious solution to the distribution of the thirty-nine derived character states used in this study if the assumption is made that all characters carry equal weight. Some justification of certain of the character polarities as entered in the data matrix will now be given. Since I had no access to specimens of most of the species used in this analysis, it was necessary to rely upon published descriptions of these organisms.

First, the loss of plate x is here believed to be a derived feature despite the absence of this plate in *Ceratocystis perneri*. This is because x is present in *Protocystites menevensis* Hicks and probably also in *Nevadaecystis americana* Ubaghs, considered on the basis of other characters to be the most anti-crownward known cornutes apart from *C. perneri*. The loss of x is in fact the only character used in this analysis which I believe to be derived in *C. perneri*, yet there is also a

TEXT-FIG. 17. Character-state tree for stem-group chordates with primitive crown-group chordates (mitrates) added. Synapomorphy scheme: 1, notochord; 2, locomotory tail; 3, loss of hydropore; 4, flexible head roof; 5, gonopore-anus opens to left of tail; 6, plate x; 7, ventral strut; 8, anterior u-plates; 9, fore tail ossicles meet in the mid-line; 10, flexible head floor; 11, loss of *u* and *ü*; 12, loss of y; 13, loss of median eye; 14, c–d articulation; **15, plate t; 16, pharynx covered by rounded integument plates; 17, loss of x**; 18, loss of v and w; **19, forward shift of buccal cavity on to d; 20, loss of i–k contact; 21, loss of e-spike**; 22, head symmetry; *23, reduced number of gill openings*; 24, loss of l-appendage; **25, plate t; 26, plate y; 27, dorsal mouth**; 28, median eye; 29, tuberculated posterior marginals; 30, heart-shaped head; *31, i–k contact*; *32, loss of symmetry*; *33, plate x*; 34, head with fringe of spines; 35, hind tail with ventral processes; 36, peripheral flange; 37, plate a excluded from strut; **38, dorsal bar**; 39, strut is not in contact with marginal plates; 40, convex ventral surface.
Characters in bold are parallelisms, italicized characters are reversals.

possibility that this species possesses a plate wax (Jefferies *et al.* 1987) which broke up in more derived cornutes into the three plates w, a, and x.

At the anterior edge of the marginal frame, between plates a and d, there are commonly found one or two smaller plates which have been called by Jefferies and Prokop (1972) v and w. In *C. perneri*, *P. menevensis*, and throughout the genus *Cothurnocystis* (excluding *T. melchiori*) both v
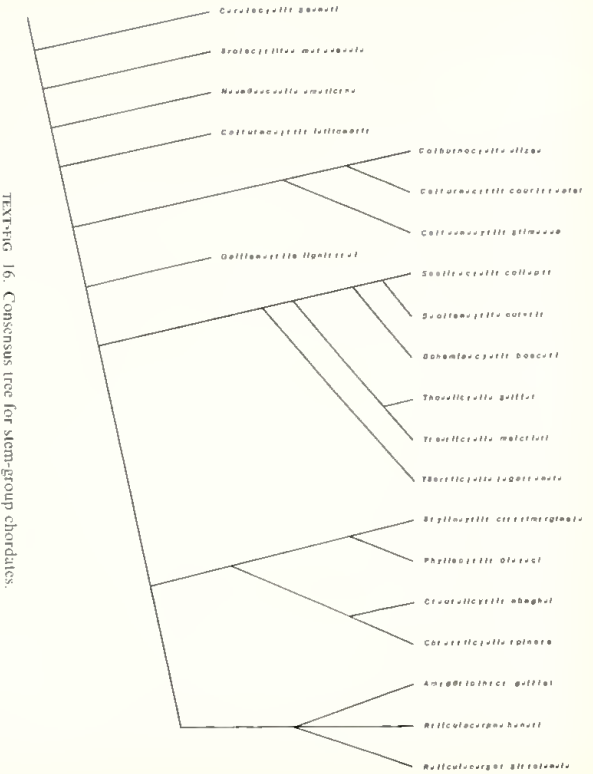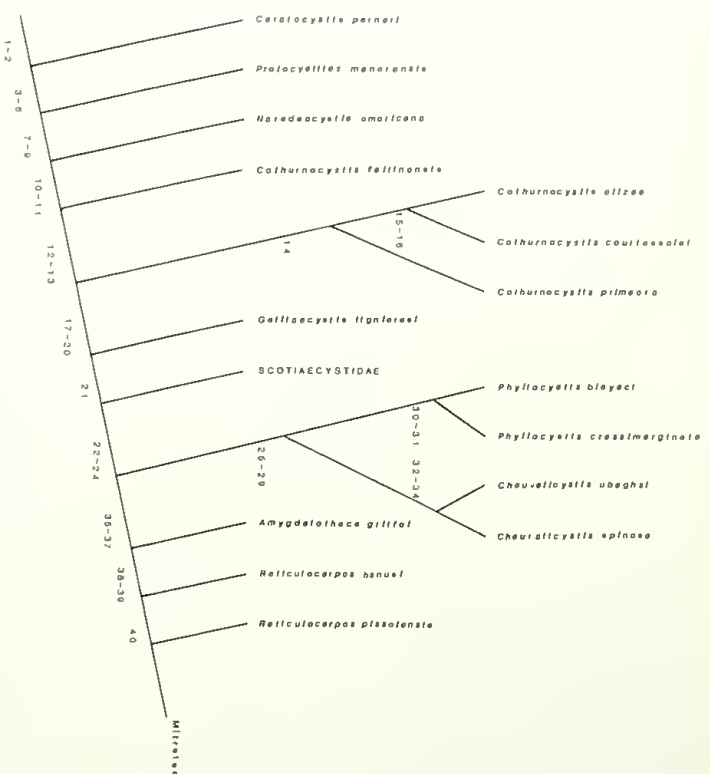
TEXT-FIG. 16. Consensus tree for stem-group chordates.

Cothurnocystis primaeva possesses a confusing array of plesiomorphic and apomorphic traits, but a clue to its systematic position may lie with the contact that the c-appendage makes with plate d. In *C. elizae* and *C. courtessolei* Ubaghs this contact is in the form of a mobile articulation (albeit more obviously so in *C. elizae*). The extent of its development in *C. primaeva* is unclear from published photographs (Ubaghs 1970). However, in the same paper Ubaghs states that the c-appendage (this digitale) is attached to plate d (his M4) 'par une articulation qui paraît peu différente'. It is therefore possible that this character, the c-d articulation, defines a group consisting of *C. elizae*, *C. courtessolei*, and *C. primaeva*. Within this group *C. elizae* and *C. courtessolei* share a plate t (acquired in parallel with the *Phyllocystis–Chauvelicystis* clade) and a covering of circular integument plates for the pharynx.

The cladogram presented in text-fig. 17 is the most parsimonious solution to the distribution of the thirty-nine derived character states used in this study if the assumption is made that all characters carry equal weight. Some justification of certain of the character polarities as entered in the data matrix will now be given. Since I had no access to specimens of most of the species used in this analysis, it was necessary to rely upon published descriptions of these organisms.

First, the loss of plate x is here believed to be a derived feature despite the absence of this plate in *Ceratocystis perneri*. This is because x is present in *Protocystites menevensis* Hicks and probably also in *Nevadaecystis americana* Ubaghs, considered on the basis of other characters to be the most anti-crownward known cornutes apart from *C. perneri*. The loss of x is in fact the only character used in this analysis which I believe to be derived in *C. perneri*, yet there is also a
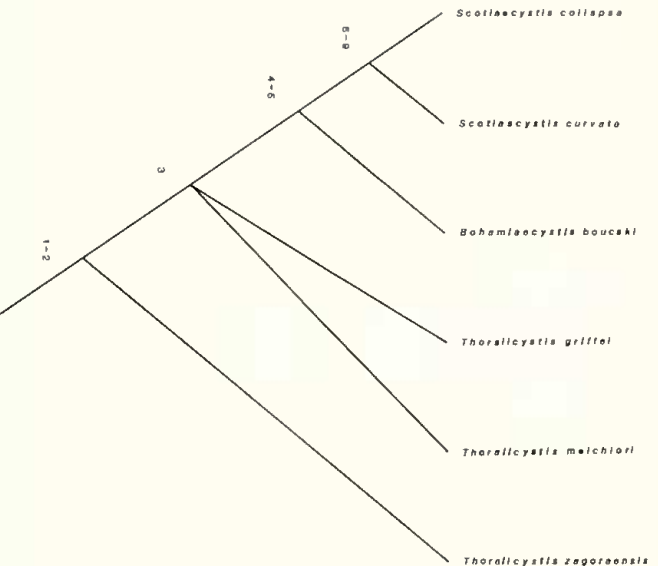
TEXT-FIG. 17. Character-state tree for stem-group chordates with primitive crown-group chordates (mitrates) added. Synapomorphy scheme: 1, notochord; 2, locomotory tail; 3, loss of hydropore; 4, flexible head roof; 5, gonopore-anus opens to left of tail; 6, plate x; 7, ventral strut; 8, anterior u-plates; 9, fore tail ossicles meet in the mid-line; 10, flexible head floor; 11, loss of *u* and *ü*; 12, loss of y; 13, loss of median eye; 14, c-d articulation; **15, plate t**; **16, pharynx covered by rounded integument plates**; **17, loss of v**; 18, loss of v and w; **19, forward shift of buccal cavity on to d**; **20, loss of i-k contact**; **21, loss of e-spike**; **22, head symmetry**; 23, *reduced number of gill openings*; 24, loss of l-appendage; **25, plate t**; **26, plate y**; **27, dorsal mouth**; 28, median eye; 29, tuberculated posterior marginals; 34, heart-shaped head; 31, i-k contact; 32, loss of symmetry; 33, plate x; 34, head with fringe of spines; 35, hind tail with ventral processes; 36, peripheral flange; 37, plate a excluded from strut; **38, dorsal bar**; 39, strut is not in contact with marginal plates; 40, convex ventral surface.

Characters in bold are synapomorphies, italicized characters are reversals.

possibility that this species possesses a plate wax (Jefferies *et al.* 1987) which broke up in more derived cornutes into the three plates w, a, and x.

At the anterior edge of the marginal frame, between plates a and d, there are commonly found one or two smaller plates which have been called by Jefferies and Prokop (1972) v and w. In *C. perneri*, *P. menevensis*, and throughout the genus *Cothurnocystis* (excluding *T. melchiori*) both v

TEXT-FIG. 18. Character-state tree for the Scotiaecystidae. Synapomorphy scheme: 1, plate s, 2, interbranchial elements; 3, dorsal mouth; 4, loss of c; 5, rearward shift of buccal cavity; 6, gonorectal canal opens into gills, 7, plate r; 8, anterior frame convex dorsally; 9, pharynx covered with rounded integument plates. Characters in bold are parallelisms, italicized characters are reversals

and w are present. This is probably the primitive condition. In *T. melchiori* and *T. griffei* (the situation in *T. zagoraensis* is unknown) one of the two plates has evidently been lost, though whether v or w cannot be determined. In all the more derived scotiaecystids, *Galliaecystis*, *Amygdalotheca, Reticulocarpos*, and in *Chauvelicystis* both plates have disappeared. The condition in *Phyllocystis* is uncertain. Because of the incompleteness of the only known specimen of *T. zagoraensis* (Chauvel 1971), it is not possible to say whether the loss of just v or w is a parallelism with reference to the cladogram given here. It could be assumed that *T. zagoraensis*, like all other scotiaecystids, is at least without one of the two plates. The most parsimonious solution (text-fig. 17) is that v and w were lost in the common ancestor of *G. lignieresi* plus all more crownward cornutes. Yet, as mentioned earlier, this implies the reappearance of one of these plates in *T. griffei* and *T. melchiori*.